INFLUENCE OF LANDSCAPE AND HABITAT CHARACTERISTICS ON OVENBIRD PAIRING SUCCESS

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ABSTRACT.—We investigated the influence of disturbance type (agriculture and silviculture) within forested landscapes, amount of forest cover within 1 km of the site, and local habitat characteristics on the pairing success of Ovenbirds (*Seiurus aurocapillus*) in central Pennsylvania during May and June 1998. Because areas with low pairing success often are inferred to have high nest predation, we also examined whether pairing and nesting success were correlated across sites. We determined the pairing status of 116 male Ovenbirds on 10 sites within contiguous mature forest. Percent of males that were paired on each site ranged from 54–92% (mean = 78%). Pairing success was negatively associated with forest cover within 1 km and positively associated with leaf litter depth. Percent bare ground also was positively correlated with forest cover within 1 km of the site. Estimates of pairing success were unrelated to Ovenbird nesting success at each site (based on 48 nests), which suggests that site-level differences in nest predation or reproductive potential are not necessarily associated with the ability of males to acquire mates. Our data suggest that pairing success of Ovenbirds in forested landscapes is not reduced by the amount of habitat loss within 1 km and is determined by local habitat rather than landscape characteristics. *Received 6 Oct. 1999, accepted 3 Feb. 2000.*

Reduced nesting success of forest birds in fragmented landscapes has been demonstrated by many researchers (Wilcove 1985, Porneluzi et al. 1993, Hoover et al. 1995, Hagan et al. 1996). Recent studies have indicated that pairing success also may be reduced by fragmentation (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998). The Ovenbird (*Seiurus aurocapillus*) is a ground nesting, area sensitive warbler (reviewed by Van Horn and Donovan 1994) that is reported to have lower pairing success in small forested tracts (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998), especially when there is little forest cover within the surrounding landscape (Van Horn et al. 1995). Explanations that have been proposed for the reduced pairing success in small forest fragments include high nest predation, low food availability, avoidance of edges by females, female-biased mortality rates, and large numbers of poor quality or young males (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998). Although empirical evidence is lacking for most of these hypotheses, data show that small forest tracts can have lower arthropod biomass in the leaf litter (Burke and Nol 1998) and lower Ovenbird nesting success (Porneluzi et al. 1993) than large forested areas. However, few studies have directly compared pairing and nesting success estimates on the same sites (but see Porneluzi et al. 1993).

Most research on pairing success of Ovenbirds has been focused on woodlots within fragmented agricultural landscapes (but see Hagan et al. 1996, Sabine et al. 1996), resulting in a limited ability to predict the impacts of disturbances on pairing success in other landscapes. Studies in fragmented silvicultural landscapes have had mixed results regarding associations between landscape characteristics and Ovenbird pairing success (Hagan et al. 1996, Sabine et al. 1996). Investigations in forested landscapes, whether impacted by silvicultural or agricultural disturbances, are still needed to determine thresholds and patterns of habitat alteration that can be tolerated by Ovenbirds.

In this study, we compared the relative influence of landscape versus local habitat characteristics on the ability of male Ovenbirds to acquire mates in contiguous forest habitat within forested landscapes. Our objectives were to (1) determine the influence of disturbance type within the landscape (agriculture and silviculture), amount of forest cover within 1 km from the study site, and local habitat characteristics on pairing success of Ovenbirds in forested landscapes of Pennsylvania

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and (2) test the association between pairing and nesting success among sites.

METHODS

Study sites.—Ten 25-ha sites within contiguous mature forest (approximately 80–110 years old) were selected in the Ridge and Valley physiographic province of central Pennsylvania (40° 40′ N, 77° 55′ W). Boundaries of each site were at least 100 m from a habitat edge. We defined our landscapes as 1 km radius circles (approximately 3.14 km^2 or 314 ha) centered on each study site. Appropriate spatial scales for landscape level studies of most Neotropical migratory birds range in size from several individual territories to a species' distribution over larger regions (Freemark et al. 1995). Because Ovenbird territories range from 0.2–1.8 ha (Van Horn and Donovan 1994), our spatial scale should be sufficiently large to be perceived as a landscape by Ovenbirds. Five sites occurred within forested landscapes disturbed by agriculture (agricultural landscapes) and those disturbed by silviculture (silvicultural landscapes). Agricultural disturbances consisted mainly of row crops with scattered hayfields, whereas silvicultural disturbances were clearcuts (less than 15 years old) with or without scattered residual trees and ranged from 7–38 ha. Sites within the two landscape types had similar amounts of forest cover, ranging from 45–82% within 1 km of the site center. At each site, at least 80% of the non-forest cover within 1 km consisted of only one disturbance type. Other disturbances within the surrounding landscape, such as roads, were similar among sites. All sites had little or no slope, relatively low horizontal heterogeneity (e.g., few internal gaps), and were 250–500 m in elevation. Sites were separated by at least 3 km to maximize independence of the 1 km radius landscapes and still be logistically feasible. Common tree species in the study area include white oak (*Quercus alba*), northern red oak (*Q. rubra*), chestnut oak (*Q. prinus*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), black gum (*Nyssa sylvatica*), black cherry (*Prunus serotina*), and hickory (*Carya* spp.).

Pairing success.—We plotted locations of all territorial males on maps of each site from mid-May to mid-June 1998 at 2–3 day intervals. We assumed that most pairing activity occurred 3–4 weeks following the arrival of Ovenbirds on sites (Gibbs and Faaborg 1990), which was in late April on our sites. From 26 May–10 June 1998, each male was observed for 90 min between 06:00–11:00 to determine pairing status (Gibbs and Faaborg 1990). This protocol has been used in investigations of Ovenbird pairing success from preincubation through nestling stages in Missouri (Gibbs and Faaborg 1990), Québec (Villard et al. 1993), New Brunswick (Sabine et al. 1996), and Ontario (Villard et al. 1993, Burke and Nol 1998). Occasionally, we could not monitor a male continuously during an observation period because of dense vegetation. In these few instances, at least four 30-min observation periods were conducted on the same morning. A male was considered paired if he tolerated a non-singing conspecific within 5 m, courtship fed, fed young, or visited a nest (Gibbs and Faaborg 1990). The observation period ended early if a male was determined to be paired. To verify the effectiveness of the 90-minute observation period, we plotted the number of paired males identified versus total elapsed observation time. At each site, an estimate of pairing success was calculated (% males paired) based on the total number of males observed per site. Over 77% of the paired males were determined to be paired within 30 minutes and over 95% within 60 minutes, suggesting that the 90 minute observation period allowed adequate time to detect evidence of pairing.

Nesting success.—Nest searching efforts for Ovenbirds began on 13 May and continued through mid-July 1998. We marked all the nests we located with numbered flagging placed more than 10 m from the nest. Nests were checked at least every 3–5 days, more often near fledging time. During a nest check, number of eggs (host and cowbird), number of nestlings, activity of parent (if seen), and any disturbance to the nest were noted. For each nest check, the nest was approached by a different route to prevent leaving a scent trail directly to the nest. If a potential nest predator was seen within 50 m of the nest, we postponed checking the nest. Each nest was determined to be successful or failed (success being at least 1 young fledged) based on length of nestling stage, destruction of nest, or detection of the fledglings. Both apparent (% nests successful) and Mayfield estimates of daily nest survival (Mayfield 1961, 1975) were calculated for each site.

Landscape and habitat characteristics.—Two landscape characteristics were examined: disturbance type within a landscape (agricultural and silvicultural) and the amount of forest cover within 1 km of the study sites. Forest cover was determined from classified thematic mapper imagery using ARC/INFO geographic information system software (ERSI 1997). To describe local habitat characteristics, we established three habitat sampling points spaced at 150 m intervals along a transect running approximately through the center of each study site. Because internal vegetative structure and composition of sites were relatively homogeneous based on our visual assessment, we felt that this sampling effort reasonably characterized each site. The following habitat variables were measured at a 0.04 ha circular plot centered on the point (modified from James and Shugart 1970): numbers of trees by species in three dbh (diameter breast height) classes (8–23 cm, 23–38 cm, and >38 cm dbh); standing dead trees in two dbh classes (15–30 cm and >30 cm), numbers of fallen logs (≥7.5 cm in diameter, ≥1.0 m long) and stumps (≥7.5 cm diameter, ≥0.25 m tall; hereafter logs and stumps are collectively referred to as woody debris), soil temperature (° C), soil pH, and soil moisture (%). Soil moisture was not measured during or less than 2–3 days following precipitation. Two 20-m perpendicular transects were established through each sampling point in north-south and east-west directions.

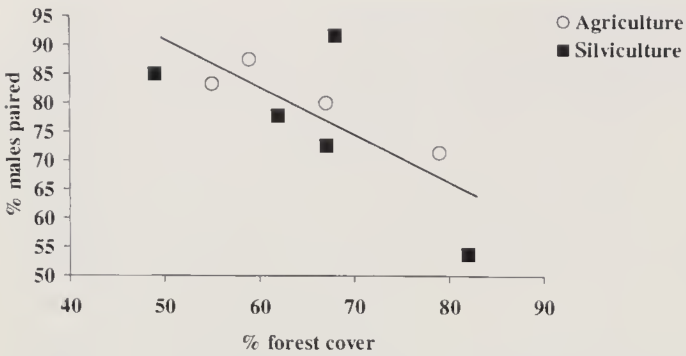

FIG 1. Relationship between Ovenbird pairing success (%) and percent forest cover within 1 km of each study site in forested landscapes disturbed by agriculture or silviculture in central Pennsylvania, 1998. The slope of the regressions is % males paired = 1.28 − 0.01 × (% forest cover).

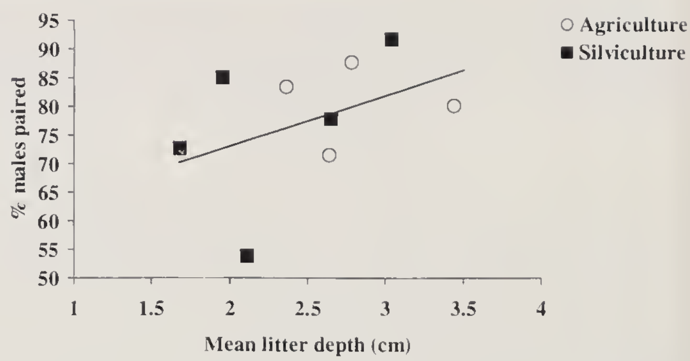

FIG 2. Relationship between Ovenbird pairing success (%) and mean litter depth (cm) at each study site within forested landscapes disturbed by agriculture or silviculture in central Pennsylvania, 1998. The slope of the regression is % males paired = 0.76 + 0.08 × (litter depth).

Percentage canopy cover (using ocular tube sightings) and litter depth (cm) were measured at 2-m intervals along these transects. Within 5 m of each sampling point, numbers of small woody stems (>0.5 m tall, <8.0 cm dbh) in size classes 0–2.5 cm and 2.5–8.0 cm (measured 10 cm above ground) were recorded by species, and percentages of ground cover (<0.5 m in height) by grass, forb, fern, moss, litter, rock, and bare ground were recorded to the nearest 5%. Measurements for each habitat characteristic were averaged over the three points within a site.

Data analysis.—Stepwise-linear regression was used to investigate the relationship between site pairing success and landscape and local habitat characteristics (Sokal and Rohlf 1995). Several highly correlated ($r > 0.7$, $n = 9$, $P < 0.01$) or collinear variables were either dropped or combined into the following new variables: total number of trees (≥8.0 cm dbh), total number of small woody stems (<8.0 cm dbh), percentage herbaceous ground cover (grass, fern, forb, and moss), and percentage nonvegetated ground cover (soil, leaf litter, and rock). Leaf litter depth, numbers of snags, amount of woody debris, soil pH, soil temperature, landscape type, and percent forest within 1.0 km also were included in our regression analysis. At each step in the analysis, a F-statistic was calculated for each independent variable in the model. Only full models with $P < 0.05$ were considered significant. Individual variables having a significance level of $P < 0.20$ were allowed to enter the model initially but later were removed if $P > 0.10$ after the inclusion of other variables. Because we had low confidence in estimating both pairing and nesting success at one site because of too few observations during the sampling period, it was excluded from analyses. Relationships between pairing and nesting success were examined using Pearson correlation analysis. Data and residuals were checked for normality, homogeneous variance, the presence of outliers and/or influential observations. All statistical analyses were conducted using SAS for Windows software, version 4.0 (SAS Institute, Inc. 1990).

RESULTS

Pairing status was determined for 116 male Ovenbirds (7–20 per site), success ranged from 54–92% of the males per site. Mean estimated pairing success was similar between contiguous forest sites within agricultural and silvicultural landscapes [81% ± 3.41 (SE) vs 76% ± 6.45, $n = 9$]. Pairing success was negatively associated with percent forest cover within 1 km (partial $R^2 = 0.52$, $F_{1,7} = 7.63$, $P = 0.03$; Fig. 1) and positively associated with leaf litter depth (partial $R^2 = 0.24$, $F_{1,7} = 5.82$, $P = 0.05$; Fig. 2) on a site (Full model: $R^2 = 0.76$, $F_{2,6} = 9.35$, $P = 0.01$). No other variables met the significance level required to be included in the model. This was also true for a regression model that included the category of small woody stems (<2.5 cm diameter) rather than the combined woody stem variable (<8.0 cm dbh). Percent forest cover within 1 km was positively correlated with percent bare ground at a site ($r = 0.66$, $n = 9$, $P = 0.04$).

Forty-eight Ovenbird nests were located (mean of 5.3 nests per site). Nesting success ranged from 40–67% (51.78 ± 3.56), and Mayfield daily survival estimates ranged from 84–98% (92.89 ± 1.41). However, pairing success on a site was unrelated to either apparent nesting success ($r = -0.49$, $n = 9$, $P > 0.05$) or Mayfield daily survival estimates ($r = 0.21$, $n = 9$, $P > 0.05$).

DISCUSSION

In contrast to previous studies that report reduced Ovenbird pairing success with increased fragmentation in highly altered landscapes (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995, Hagan et al. 1996, Burke and Nol 1998), we found the opposite pattern. We suspect that this difference is due to the fact that all of our landscapes were heavily forested relative to those other areas and, thus, probably were not disturbed enough to compromise pairing success. In forested landscapes in New Brunswick, Sabine and coworkers (1996) also failed to detect a negative association between Ovenbird pairing success and forest area. Even though landscape characteristics, such as type of disturbance and amount of forest cover, are known to influence bird communities (Andrén 1992, Friesen et al. 1995, Bayne and Hobson 1997, Donovan et al. 1997), the significant association we detected between forest cover and bare ground on sites raises the possibility that the ability of males to acquire mates was a function of characteristics at the local scale only.

We suggest that observed patterns of pairing success are best explained by local differences in habitat characteristics among sites. Leaf litter depth and bare ground, in particular, should be important because Ovenbirds forage by gathering invertebrates from leaf litter on the forest floor (Holmes and Robinson 1988, Van Horn and Donovan 1994). Indeed, previous workers showed that litter depth may be a cue used by females to select nest sites (Van Horn and Donovan 1994), and litter depth is deeper in occupied Ovenbird territories versus random locations (Burke and Nol 1998) and territories of paired versus unpaired males (Van Horn et al. 1995). Ovenbirds may use structural habitat cues, such as litter depth, to assess habitat quality and prey abundance (Smith and Shugart 1987). Leaf litter depth is thought to indicate invertebrate biomass, which was greater in occupied Ovenbird territories than in random locations in Ontario (Smith and Shugart 1987, Burke and Nol 1998; but see Sabine et al. 1996). In addition, Burke and Nol (1998) reported lower pairing success in fragments with significantly more bare ground and less developed seedling and shrub layers than in large forest tracts. Thus, we believe that the negative relationship that we observed between forest cover and pairing success may represent a statistical artifact rather than an ecological relationship.

A link between pairing and nesting success has been proposed several times (Gibbs and Faaborg 1990, Villard et al. 1993) and is thought to contribute to low pairing success on small forest fragments. Because small forest fragments generally have higher rates of nest predation than large forest tracts, researchers have suggested that a male-biased sex ratio may result if females avoided small fragments or were killed during incubation or brooding. Presumably, a similar situation might occur in forested landscapes that differed in nesting success. Despite variation in both Ovenbird pairing and nesting success among our study sites, pairing and nesting success were unrelated. This suggests that site-level differences in nesting success were not responsible for variation in the ability of males to acquire mates. However, associations between pairing and nesting success may be temporally offset, where low observed pairing success may reflect prior, not current, elevated predation rates.

Our data suggest that in landscapes with extensive and contiguous forest, pairing success of Ovenbirds is not reduced by limited amounts of habitat loss in the surrounding landscape and is a function of local habitat rather than landscape characteristics. Because we detected no correlation between pairing and nesting success for Ovenbirds across sites, differences in nesting success failed to explain the observed variation in Ovenbird pairing success. Although our sample sizes of both sites and nests were relatively small and limited to only one field season, the absence of a clear relationship between pairing and nesting success leads us to caution against the use of pairing success as an index to reproductive potential. Previous studies of forest birds in highly modified landscapes have given us considerable insight into the impacts of landscape alteration on breeding bird pairing and nesting success. Examination of these phenomena in relatively forested landscapes is essential to understand patterns and thresholds of habitat alteration that can be tolerated by sensitive forest birds.

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